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OXYGEN CONSUMPTION OF THE PURPLE SEA URCHIN WITH SPECIAL REFERENCE TO THE REPRODUCTIVE CYCLE[1]

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Steen (1965) reported that the rate of oxygen consumption per unit weight (Q_{O_2}) of intact sea urchins is about one tenth the theoretical value calculated from summed tissue respiration and attributed this discrepancy to inefficiencies in the movement of external sea water and internal respiratory media (ambulacral and perivisceral fluids) over respiratory epithelia.

Giese, Farmanfarmaian, Hilden and Doezema (1966) reported that the Q_{O_2} per unit weight remained the same throughout the annual reproductive cycle of the purple sea urchin (*Strongylocentrotus purpuratus*) at the peak of which the organic content of the body approximately doubles. The increase in organic material in the body is not taken into account by a Q_{O_2} so measured because the specific gravity of the organic matter is very similar to that of the body fluid displaced as the gonads grow: the total volume of a sea urchin remains much the same during the reproductive cycle except for growth. To relate the oxygen consumption of the sea urchin to its organic content the Q_{O_2} was determined per unit nitrogen. On this basis the Q_{O_2} declined during growth of the gonads, minimal values' being found at the peak of the reproductive cycle when the gonads were of maximal size. The authors postulated that the oxygen consumption of the intact sea urchin is limited by the respiratory surface and by inefficient convective oxygen transport from ambient sea water to internal tissues. When the gonads reach maximal size the supply of oxygen to the tissues is poorest. As indirect evidence for this contention they point out that the sum of oxygen consumption of the individual body components measured in a dissected sea urchin is always greater than that for the intact organism.

Johansen and Vadas (1967) studied oxygen consumption in relation to ambient and perivisceral fluid oxygen partial pressure (ppO_2) in three sea urchins of the genus *Strongylocentrotus: S. purpuratus, S. franciscanus* and *S. drobachiensis.* They concluded that the Q_{O_2} measured directly is more closely related to internal than external ppO_2. They did not, however, study the relation between the reproductive state and oxygen consumption.

The present study aims to elucidate, by polarographic oxygen electrode measurements of the perivisceral fluid oxygen partial pressure ($PvfO_2$) and the ambient sea water oxygen partial pressure (AO_2), the apparent paradoxical decline in Q_{O_2} per unit nitrogen with increase in organic matter of the purple sea urchin during the course of the reproductive cycle. Also considered are the effects of

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body size, air exposure, and the possible relative contribution of the body wall to the total oxygen consumption of an intact sea urchin.

Materials and Methods

Collecting sites

The sea urchins were collected monthly or bi-monthly on the San Mateo County coast, California (37°20′ N. Latitude) from populations in similar low intertidal habitats at three locations: Pigeon Point, Bean Hollow Beach, and Pescadero Point. They were taken to the laboratory in wet algae or aerated sea water and kept in aquaria containing filtered, aerated sea water at 13 ± 3° C. They were starved for one to three weeks prior to use to minimize the effect of varied nutritional state and contamination with fecal material. Oxygen consumption of several freshly collected animals was determined for comparison with oxygen consumption of the starved individuals.

Six sea urchins were sacrificed from each collection to determine the gonad index (wet weight of gonads divided by the wet weight of the body) as an indication of the reproductive condition of the population. For this purpose each animal was blotted on paper toweling for 30 seconds and weighed within ±0.1 gram on a triple beam balance. Then, following draining of the perivisceral fluid, the gonads were removed, blotted and weighed. In some cases the body wall indices were determined following removal of the Aristotle's lantern and the gut.

Oxygen electrode technique

The electrode used for monitoring the ambient oxygen partial pressure (AO_2) in the laboratory was a Beckman #315780 Clark electrode (Clark, 1956) coupled to the Beckman Model 160 Gas Analyzer (Beckman Instruments, Inc., Spinco Division, Palo Alto, California). This electrode was inserted through a sleeve of Tygon tubing in a 3/8-inch hole drilled in the Bakelite top of a specimen jar of desired size. This closed jar, immersed in a circulating water bath at the desired temperature, served as the respirometric chamber. As ambient oxygen was depleted by the sea urchin in the closed chamber, the Q_{O_2} (μl/g/hr) was calculated according to the equation: $Q_{O_2} = [\text{Vol. } O_2 \text{ consumed (ml/l)} \times \text{Vol. ambient water (l)}]/[\text{Times (hrs)} \times \text{Wet weight (g)}] \times 1{,}000$. The volume of O_2 consumed was calculated by converting the change in AO_2 in the vessel during the experiment from mm Hg to ml/l using the tables of Green and Carritt (1967).

A circulating water bath (Forma Scientific, Inc., #2095-2 refrigerated the external bath), was placed above the magnetic stirring unit. Water temperature was regulated to within 0.1° C in the respirometer chamber. The stirring bar placed below the test animal kept the ambient water in constant circulation during the experiment, equilibrating oxygen tension and temperature throughout the vessel (Figure 1).

Filtered sea water was used in the respirometric vessel, and was brought to equilibrium with air by gassing through a fine air stone for at least 30 minutes. Giese *et al.* (1966) showed microbial respiration to be a negligible factor at 13° C and below, so the use of antibiotics was suspended in all but the experiments at

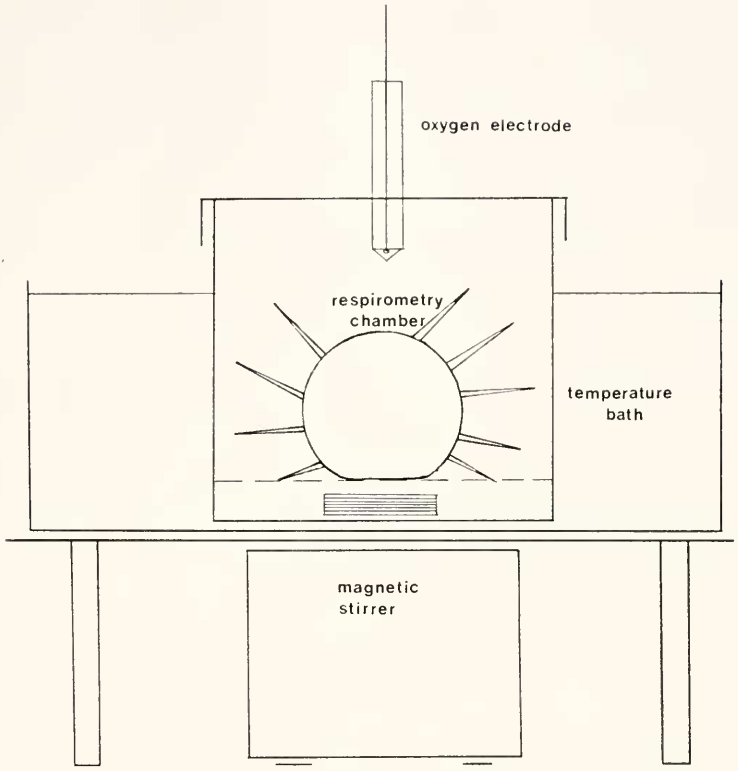

FIGURE 1. Representation of external water temperature bath and respirometric apparatus.

23° C. The oxygen consumption was about the same whether buffer was added to sea water or omitted (Lutz, 1930; Childress, 1968), though some carbon dioxide accumulation accompanied by a pH change occurs (Tang, 1933). Therefore buffering was also discontinued. The gas phase was eliminated from the chamber by the addition of sea water through the electrode port in the lid of the chamber prior to insertion of the electrode.

Chamber sizes were selected to provide a full-scale response (from 160 mm Hg to 0 mm Hg) in a period of five to six hours. Contrary to the findings of Johansen and Vadas (1967), our test animals failed to recover from exposure to an AO_2 below 80 mm Hg for more than one or two hours and generally died three or four days after the experiment. For this reason, only data from experiments of two hours duration are cited. Calibration of the electrode was checked before and after each run. If pre-experiment and post-experiment calibrations differed from each other by more than 5%, the data were discarded.

Prior to each oxygen depletion experiment, animals placed in the respirometric vessel were kept in aerated sea water for 15 to 30 minutes to achieve temperature equilibration with ambient sea water and to minimize the effects of possible excitation resulting from handling (Halcrow and Boyd, 1967; Childress, 1968).

Determinations of the ppO_2 of perivisceral fluid and gonad tissue were made with a Clark needle oxygen electrode (#17365), Instrumentation Laboratory, Lexington, Massachusetts. The electrode is constructed within a 4-3/4 inch long hollow stainless steel shaft of 0.2 mm diameter, and is covered with a tubular polypropylene membrane, closed at one end, containing a small amount of electrolyte gel. Because the electrode is of small diameter, is flexible, and is relatively rugged in its construction, it is ideally suited to investigations of this kind. The electrode was coupled to the Beckman Model 160 gas analyzer. Studies of tissue ppO_2 with this instrument must be analyzed with care, as electrophoretic protein deposition, while probing tissues, may "poison" the electrode and change its calibration (Silver, 1966). However, determinations of perivisceral fluid ppO_2, which has a low protein content, can be made without concern. The needle oxygen electrode was used in conjunction with an open chamber, which facilitated placement of the electrode into a known locus in the sea urchin. A 2 mm hole drilled in the test of the sea urchin allowed for the entry of the electrode into the perivisceral coelom. As clotting of the perivisceral fluid sealed the shaft of the electrode to the body wall, little exchange between perivisceral fluid and ambient sea water occurred through the hole.

Ambient oxygen partial pressures were regulated by gassing the surrounding sea water with air, oxygen, or nitrogen, and were monitored with a YSI Model 54 Oxygen Meter and YSI #5034 oxygen probe (Yellow Springs Instrument Company, Yellow Springs, Ohio).

Experimental Results

Before determining the oxygen consumption during the reproductive cycle it was necessary to investigate the effects of some relevant variables on the rate of oxygen consumption. The present results were related to previous manometric studies by performing experiments in sequence on the same individuals with both manometry and oxygen electrodes.

Oxygen consumption at different ambient oxygen partial pressures

With an oxygen electrode in a closed system the ambient oxygen partial pressure (AO_2) falls as oxygen is consumed by the animal. It was therefore necessary to determine the effect of oxygen partial pressures (ppO_2) on oxygen consumption rate. A typical oxygen depletion curve for *S. purpuratus* (Figure 2 and Table I) indicates complete conformity between Q_{O_2} and ppO_2 to 5–10 mm Hg.

During the first two hours of each trial the AO_2 was depleted to the level of 80–100 mm Hg (Figure 2), equivalent to 3.0 to 3.7 ml/l at 13° C. Low environmental partial pressures of oxygen are rarely encountered by *S. purpuratus* in nature In fact the environmental partial pressures are seldom much below the air saturation level (Horne, 1969). An argument could thus be made for calculating the oxygen consumption rate on the basis of the earlier part of the depletion curve rather than the two hours chosen for this purpose, because the higher AO_2 more nearly represents the conditions to which the sea urchins are generally exposed in nature.

The oxygen consumption rates represented in Figure 3 (based on two-hour

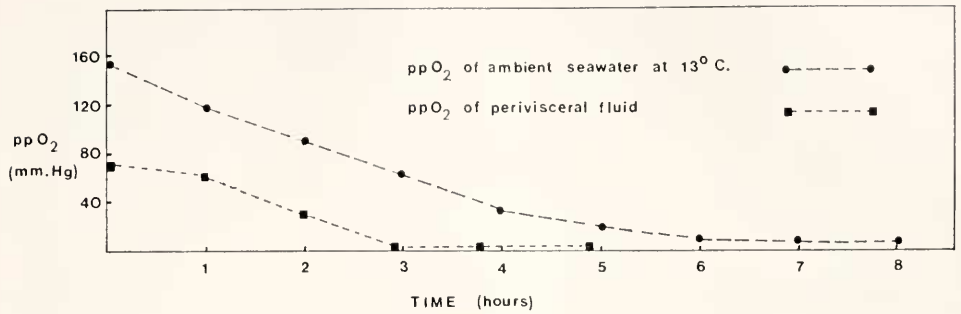

FIGURE 2. Typical oxygen depletion curve for *S. purpuratus* in a closed respirometer. Top line (dots) indicates ambient oxygen tension (AO_2) as a function of time. Bottom line (squares) represents perivisceral fluid oxygen tension ($PvfO_2$) during the same oxygen depletion run.

oxygen depletion experiments) are in essential agreement with the results of Johansen and Vadas (1967) and the oxygen depletion curves are similar to theirs of *S. purpuratus*. However, these authors did not indicate from which part of the oxygen depletion curve their Q_{O_2} values were calculated.

Comparison of manometry and oxygen electrodes

Oxygen consumption rates measured with Warburg manometry are uniformly higher than those obtained with the oxygen electrode system for equal sized sea urchins (Figure 3), probably because a constant AO_2 is maintained in the water by equilibration with the reservoir of air in the vessel, though possibly excitation occurs from the rocking of the manometers. Farmanfarmaian (1959) reports a constant rate of oxygen consumption throughout each two to three hour trial.

Seasonal and temperature background as it affects oxygen consumption

Data of seasonal effects on oxygen consumption in *S. purpuratus* have been collected only incidentally to other studies. Seasonal aspects of oxygen consumption might include the effects of factors considered later which change with season, such as temperature, nutrition, and reproductive state. Farmanfarmaian and

TABLE I

Q_{O_2} for three S. purpuratus *calculated for each hour during a five or six-hour run, on the basis of the mean ppO_2 in the chamber during each hour. All experiments at 13° C, Q_{O_2} in μl/g/hr.*

Hour	Q_{O_2} (31.5 g)	Q_{O_2} (67.1 g)	Q_{O_2} (89.0 g)
1	17.65	13.58	9.70
2	7.77	6.74	5.15
3	7.05	5.40	4.24
4	6.85	4.35	3.55
5	3.94	2.88	1.90
6		0.75	0.77

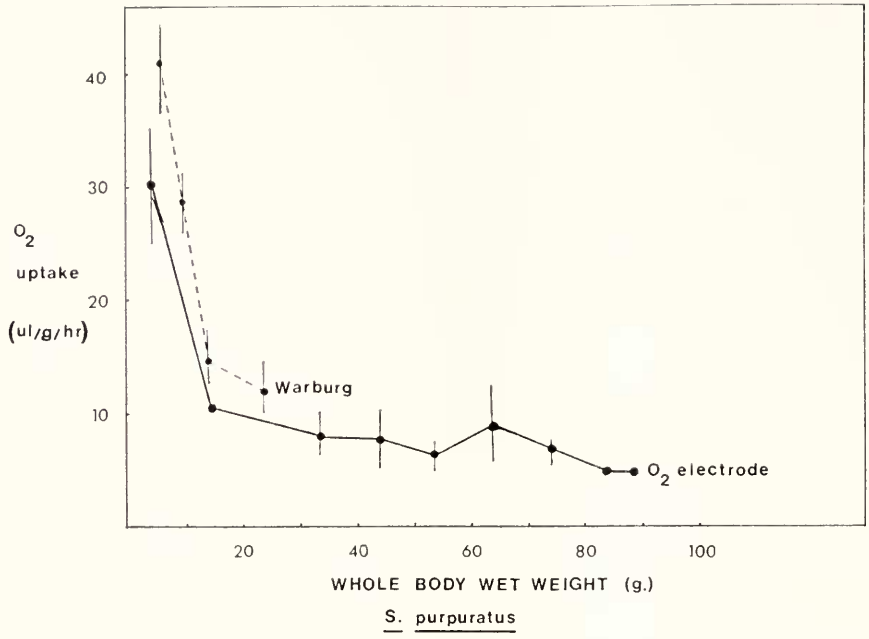

FIGURE 3. Oxygen consumption in *S. purpuratus* at 13° C as a function of whole body wet weight. Top line represents Warburg manometric data. Bottom line shows data obtained with oxygen electrode apparatus described in text. Vertical lines are single standard deviation units above and below the mean.

Giese (1963) found acclimation to lower temperatures (5° C) in the purple sea urchin over a period of 15 to 30 days, but no acclimation to higher temperatures, and the animals die when kept at temperatures above 23.5° C. Ulbricht and Pritchard (1972) found metabolic rate independence in *S. purpuratus* between 12 and 20° C. The present investigations were conducted at 13° C with sea urchins which had been held at that temperature for one to three weeks prior to use.

Tidal and circadian rhythms and oxygen consumption

Ulbricht and Pritchard (1972) studied the effect of tidal cycles and time of day on oxygen consumption in *S. purpuratus,* using oxygen depletion experiments of 36 hours' duration. They found no indication that tidal cycle or time of day affects the oxygen consumption rate. No evidence to the contrary was found in the present study in several experiments of 24 hours' duration.

Effect of oxygen enrichment on oxygen consumption

Two oxygen electrode studies demonstrated that oxygen consumption of *S. purpuratus* at ppO_2 above air saturation is greater than in air-saturated sea water. Thus when pure oxygen was bubbled through filtered sea water at 13° C to achieve a starting AO_2 of 390 to 400 mm Hg, 2-hour determinations with a 40.9 g

S. purpuratus yielded Q_{O_2} values of 18.4 to 18.6 μl/g/hr. AO_2 during the 2-hour run was depleted from 390 mm Hg to 290 mm Hg. These rates are about twice the Q_{O_2} for a 40 g *S. purpuratus* in air-saturated sea water at this temperautre (Figure 3).

Oxygen partial pressure of perivisceral fluid as a function of oxygen partial pressure of ambient sea water

Representative data obtained with a needle oxygen electrode (Figure 2) indicate a $PvfO_2$ between 40 and 60 mm Hg for 60 to 89 g *S. purpuratus* in sea water near air saturation (150 mm Hg). In a series of tests for sea urchins of similar size the $PvfO_2$ 13° C was found to vary between 23 and 54 mm Hg. In a series of tests on sea urchins of differing size, the $PvfO_2$ was found to increase directly with increase in size (Figure 4).

As the AO_2 falls during depletion of the oxygen in a closed vessel containing a sea urchin, the $PvfO_2$ changes little during the first 25 minutes following which it falls in parallel with the AO_2. $PvfO_2$ falls to zero when AO_2 falls to about 75–80 mm, *i.e.* about one half of the air-saturation level (Figure 2). With the needle oxygen electrode the initial temporary rise in $PvfO_2$ reported by Johansen and Vadas (1967) was not observed here.

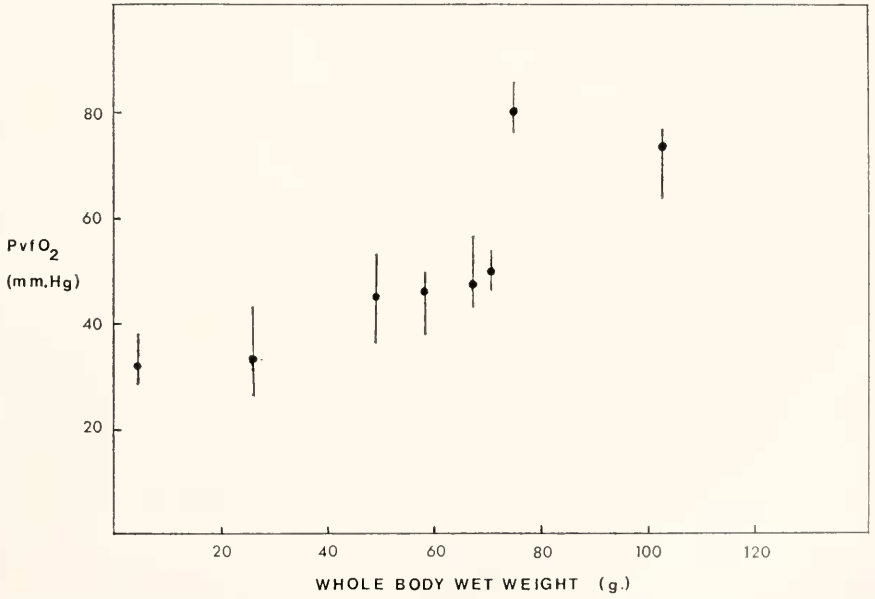

FIGURE 4. Perivisceral fluid ppO_2 in *S. purpuratus* as a function of whole body wet weight at 13° C. The coefficient of correlation (r) of 0.823 indicates a fairly high degree of relationship between these two factors. Points are mean PvO_2. High and low extremes during each experiment are indicated by vertical lines. Least squares analysis yields a y-intercept of 23.9, and a slope of 0.489.

Effect of body size on oxygen consumption

The relationship of oxygen consumption to body size in animals is usually expressed by the equation: metabolism = k·body weight^b where k and b are constants (Prosser and Brown, 1965; Newell, 1970). The value of b for larger metazoan poikilotherms is often quoted as 0.73, or intermediate between proportionality to weight and proportionality to surface area (Whitford and Hutchinson, 1967). This relationship is characteristic of most invertebrates (Zeuthen, 1947), including echinoderms (Farmanfarmaian, 1959, 1966).

Although total oxygen consumption is higher in larger *S. purpuratus,* the rate of oxygen consumption (expressed as Q_{O_2}) is higher for smaller animals than for their larger counterparts (Giese, 1966, Figure 3). The value of b for *S. purpuratus* over the wet weight range of 10 to 110 grams is approximately 0.65, a value in agreement with the findings of McPherson (1968) for *Eucidaris tribuloides.* As mentioned by Giese (1966), this makes body size (along with the nutritional state) an important factor to control in comparisons of oxygen consumption data for effects of different factors.

Oxygen consumption of isolated body wall

Using isolated body walls from *S. purpuratus* in the 10 to 100 g range, body wall oxygen consumption was found to be about four times the Q_{O_2} for the intact animal (Figure 5). Although the data are insufficient for statistical analysis, the Q_{O_2} for body wall tissue from small individuals was higher than that from large individuals (Table II). A decrease of the respiratory rates of the individual tissues, with an increase in size of the animal, may account for the lower Q_{O_2} of large as compared with small *S. purpuratus.* The Q_{O_2} of the dissected body wall may exceed the Q_{O_2} for the whole animal because both internal and external body wall surfaces are exposed to sea water near saturation with air, while only the external surface in the intact animal is so exposed; the internal surface of the intact animal is exposed to fluid containing only about one half to one fifth this much oxygen. Furthermore, the ambient fluid is circulated past the surface of the dissected body wall much more rapidly than in an intact animal, thereby considerably increasing the oxygen available to the tissue.

It is also possible that the isolated body wall had a higher oxygen consumption than in the intact animal because of a soluble "injury factor" diffusing from the dissected tissues. To test this the filtered and aerated supernatant from the crushed body wall leached in sea water for an hour was added to sea urchins. No detectable change in slope of the oxygen depletion curve was observed after such additions (three experiments). Thus, the Q_{O_2} for intact sea urchins before addition of extract averaged 10.2 μl/g/hr, while after addition of extract it averaged 10.4 μl/g/hr.

Effect of exposure of sea urchins to air

Since air contains 40 times as much oxygen as sea water, it might be reasoned that a sea urchin could survive in air provided it was kept moist. This appears

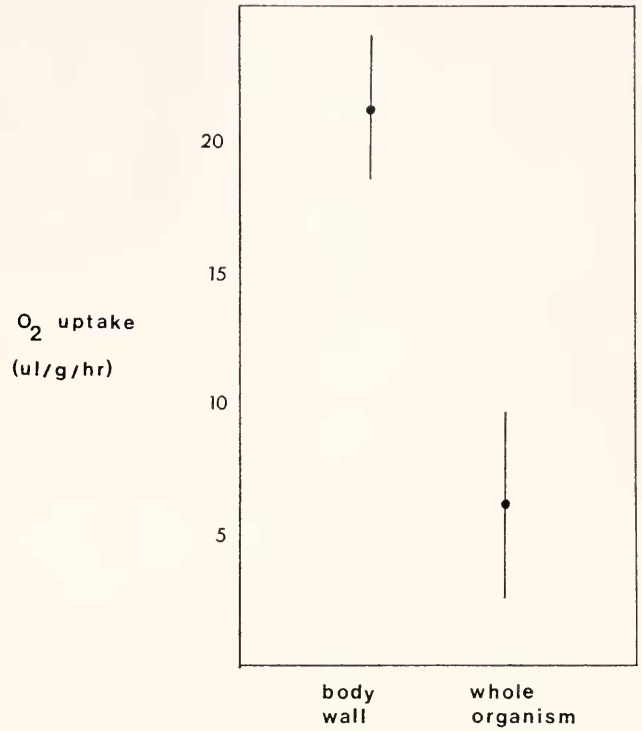

FIGURE 5. Comparison of oxygen consumption in intact *S. purpuratus* and the body wall component only; four trials at 13° C.

to be the case, although experiments with the oxygen needle electrode demonstrate that the $PvfO_2$ of sea urchins in air falls to almost zero after three hours exposure and remains there afterwards (Figure 6). This indicates the interruption of oxygen transport through the structures of the body wall of a sea urchin in air. These data are in agreement with those of Johansen and Vadas (1967) for *S. purpuratus*. Assuming no entry of oxygen from ambient sea water to ambulacral

TABLE II

Q_{O_2} (μl/g/hr) of the body wall as a function of body size (wet weight) in S. purpuratus *at 13° C.*

Wet weight (g)	Body wall index	Whole body Q_{O_2}	Body wall Q_{O_2}
10.5	61.5	28.6	39.0
62.9	44.2	11.1	30.7
72.3	41.2	6.49	24.9
83.0	44.2	5.78	23.4
94.6	48.3	4.57	18.2
96.1	46.3	8.85	18.2

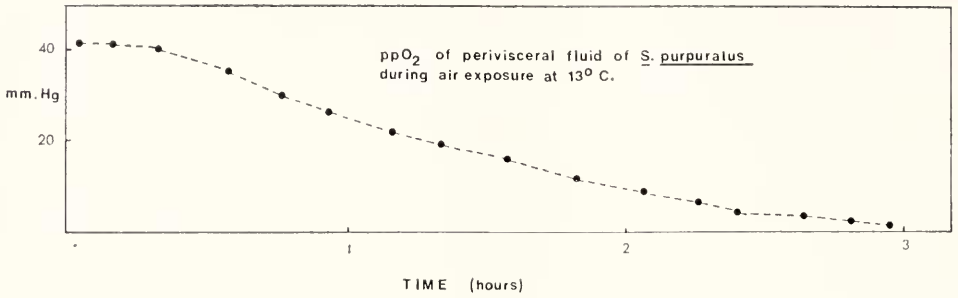

FIGURE 6. Needle electrode data indicating the change in perivisceral fluid oxygen tension with time in *S. purpuratus* in air at 13° C.

fluid during air exposure, on the basis of the oxygen depletion curve, the Q_{O_2} for the internal tissue is calculated to be 0.64 μl/g/hr. This is about one-tenth the expected Q_{O_2} for tissue of a sea urchin of this size, and is about one-half that for perivisceral fluid outside of the animal measured manometrically by Giese, Farmanfarmaian, Hilden and Doezema (1966).

Oxygen transport to the ambulacral system was stopped in another way by covering a sea urchin with Vaseline (Table III), a procedure which totally obstructs the exchange of oxygen with the body wall epithelium and tube feet (Farmanfarmaian, 1966). During this experiment the $PvfO_2$ was depleted from 40 mm Hg to zero in about 1.5 hours, yielding a Q_{O_2} for internal tissues of 1.18 μl/g/hr. This value and the value from sea urchins exposed to air indicate that the Q_{O_2} of the internal tissues probably accounts for no more than 10% of the total oxygen consumption of the intact *S. purpuratus*.

Although oxygen transport into the perivisceral coelom is interrupted during air exposure (Figure 6), the outer body wall obtains ample oxygen so long as the respiratory surface remains moist. Sea urchins used in the 3 hour air exposure experiments recover completely when returned to aquaria.

Oxygen consumption during the reproductive cycle

As measured by gonad index (Lasker and Giese, 1954) the reproductive cycle of *S. purpuratus* on the central California coast reaches its peak between November and January; spawnout occurs between January and March (Giese,

TABLE III

Comparison of the Q_{O_2} of internal tissues in the intact S. purpuratus *at 13° C, one animal in air, the other covered with Vaseline; Q_{O_2} for a whole animal in sea water at bottom.*

	Wet weight (g)	Q_{O_2}
Air exposure	46.8	0.64
Vaseline-covered	36.2	1.18
Whole body Q_{O_2} in sea water	38.7	8.9

1959). The gonad index reaches its lowest value between March and May. A maximal gonad index of about 25 has been measured for some members of a population near the peak, but the average for the present season near the peak was about 15; spawning is asynchronous—usually some individuals had spawned out when others were reaching the peak gonad size. The minimal gonad index varies between 3 and 5, but previous studies recorded values as low as 1.

The oxygen consumption of sea urchins was measured at various times during the reproductive cycle and the urchins were then dissected and the gonad index determined. The oxygen consumption rates were found to vary considerably for animals with both high and low gonad index (Table IV). Part of this variation is a result of the variation in size. However, animals of the same size and same gonad index varied considerably in their oxygen consumption. Since the factors considered to influence oxygen consumption were tested and taken into account in preparing for the present measurements, some factor other than those considered, and other than gonad index, must introduce the variability. That factor has remained elusive.

The major point of these experiments, however, was to determine whether the gonads were contributing appreciably to the oxygen consumption since they account for most of the doubling in organic matter in a gravid sea urchin. Tests of the gonads with the needle oxygen electrode at various times during the reproductive cycle in all cases gave ppO_2 values between 0.0 to 10.0 mm Hg (Figure 7). The method is inadequate to tell whether the higher values are for smaller gonads, because the same gonad gives different values on repeated trials.

Similarly, when measurements were made of the $PvfO_2$, an inverse correlation was found between $PvfO_2$ and weight of the sea urchin (Figure 4), rather than with gonad index, but the difficulties in making measurements with the oxygen micro electrode when the coelom is filled with tissue made it difficult to get reliable data for gravid sea urchins. The data are therefore mainly from specimens of low gonad index. These data indicate that the $PvfO_2$ is between 20 and 50% of the sea water saturation values of oxygen.

TABLE IV

The whole body Q_{O_2} as a function of gonad index in S. purpuratus *at 13° C. Least squares analysis gives Y intercept of 9.76 and a slope of −0.117, indicating little correlation between gonad index and oxygen consumption (Q_{O_2}).*

Gonad index	Wet weight	Q_{O_2}	Gonad index	Wet weight	Q_{O_2}
20.1	54.7	6.9	8.9	28.1	6.8
18.1	112.1	7.8	8.7	62.9	11.1
15.4	33.2	8.7	7.4	33.4	11.5
14.5	92.4	7.9	5.2	72.1	6.0
14.1	110.3	8.4	5.2	59.3	7.8
13.2	93.5	4.5	4.2	89.0	4.6
12.5	43.5	12.5	3.8	38.6	9.6
12.3	38.7	8.9	3.1	39.3	16.9
9.7	19.3	6.7	2.1	59.6	5.5
9.0	44.2	9.1	1.5	46.5	11.9

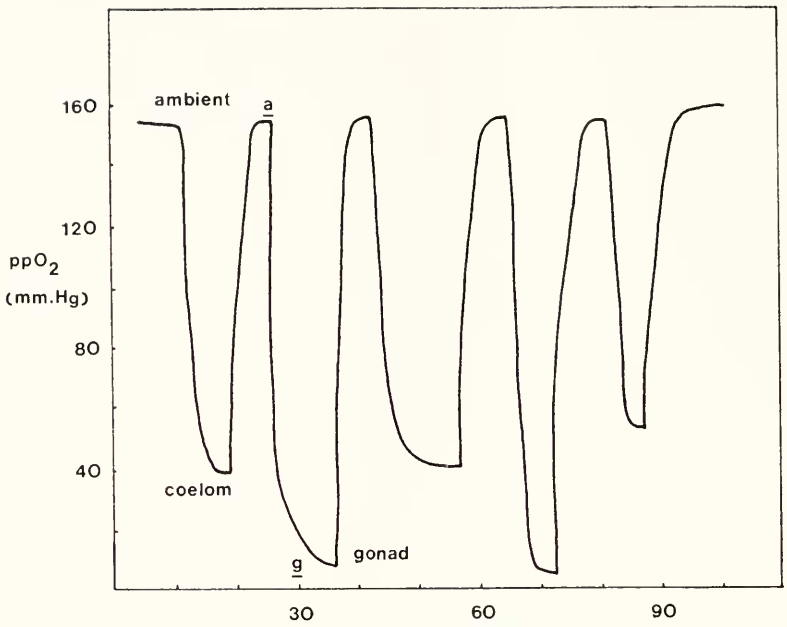

FIGURE 7. Representative data obtained with the needle oxygen electrode. Beginning with calibration in air saturation (157 mm Hg) the electrode is inserted through a hole drilled through the test into the perivisceral coelom. The perivisceral fluid oxygen partial pressure (PvO_2) is determined when a stable reading is achieved. The electrode is then withdrawn into ambient sea water and the calibration is checked (a). When stable at air saturation, the electrode is reinserted into gonad tissue (g), and a reading is made when a stable output is once again obtained. Two additional readings of PvO_2 and one of gonad tissue are represented.

DISCUSSION

The main purpose of the present study was to ascertain the reason for the finding that the rate of oxygen consumption (Q_{O_2}) of the purple sea urchin determined manometrically does not increase with increase in gonad size at the peak of the reproductive cycle when the total organic content of the body just about doubles (Giese, Farmanfarmaian, Hilden, and Doezema, 1966). The authors of the study quoted demonstrated that when the oxygen consumption of the body components was separately determined the summated Q_{O_2} for the entire body did increase with the increase in size of the gonads. They postulated that the limiting factor for such increased oxygen consumption in intact animals must be the lack of oxygen in the perivisceral fluid to supply the oxygen to the internal tissues. In other words, only the superficial cells in the large gonads were probably adequately supplied with oxygen and the bulk of the tissue had to take care of its metabolic needs by anaerobic processes.

The present study using oxygen electrode techniques corroborates the finding of a lack of correspondence between the size of the gonad and the rate of oxygen consumption which appears to depend mainly upon the size of the animal, other things being equal. The present study also supplies the information on the partial

pressure of oxygen in the perivisceral fluid bathing the tissues, indicating that indeed it is low—at about 20 to 50% of the air-saturation value—and limits the rate of respiration of the internal tissues, which probably contribute only about 10 per cent of the total oxygen consumption of the sea urchin body. Unless oxygen is continuously supplied the partial pressure of oxygen falls as the tissues deplete it. Furthermore, measurements with a needle oxygen electrode demonstrate that the partial pressure of oxygen inside of tissues such as the gonad is indeed very low, between 10 mm Hg and zero. Such tissues are therefore internally anaerobic. Little is known of the anaerobic metabolism of tissues of the purple sea urchin, a study of which might be quite rewarding. Thus, regardless of the increase in mass and organic content (as measured by the total nitrogen of the gonads as they near the peak of the reproductive cycle), no corresponding oxygen consumption is found nor is it to be expected considering the limiting oxygen supply in the perivisceral fluid demonstrated here. It is possible that the variation in the measurements of perivisceral fluid oxygen may be a result of different locations of the electrode in the coelom. Owing to the poor circulation of the perivisceral fluid in the coelom, it is possible that next to the tissues where oxygen consumption occurs, the $PvfO_2$ is much lower than in the bulk of the fluid.

In the majority of the present experiments the oxygen depletion curve levels off before the last traces of oxygen have been consumed, a phenomenon also reported by Johansen and Vadas (1967) in *S. purpuratus* and *S. droebachiensis*, and by Mangum, Kushins and Sassaman (1970) in many invertebrate species. Apparently the animal has either reverted completely to anaerobic respiration at these low ambient oxygen partial pressures, or aerobic respiration is at such low levels as to be undetectable with the oxygen electrode.

The value for oxygen consumption of the purple sea urchin, *S. purpuratus*, determined by the oxygen electrode is somewhat lower than that determined by the manometric method, though both are of the same order of magnitude. The higher values for the manometric method are probably attributable to the higher oxygen partial pressure of the fluid continuously mixed with the air in the chamber. In the closed and fluid-filled chamber used with the oxygen electrode, the partial pressure of oxygen around the experimental animal declines at a rapid rate.

The present data provide information on a number of problems other than the relation between oxygen consumption and the reproductive cycle. Johansen and Vadas (1967) report that *S. purpuratus* regulates its oxygen consumption rate down to AO_2 levels of 60 to 70 mm Hg, and conclude that the Q_{O_2} is closely related to the ppO_2 of internal tissues and to the AO_2. They also consider the great variation of $PvfO_2$ of sea urchins in nature as evidence of metabolic regulation in *S. purpuratus*, but do not speak to the effect of body size on the $PvfO_2$. The results of this investigation contradict these statements. We find that $PvfO_2$ correlates inversely with the relative amount of body wall tissue (body wall index, Figure 4) in *S. purpuratus*, and therefore, with the Q_{O_2} of the intact animal. In other words, the $PvfO_2$ in small sea urchins is low in the presence of proportionally more body wall tissue of relatively high Q_{O_2} compared with large individuals. Apparently the important determinant of Q_{O_2} in *S. purpuratus* is the response of body wall tissue to the AO_2. Specimens of *S. purpuratus* and the dissected body wall component are both strict conformers and respire in direct

proportion to the availability of environmental oxygen. The relatively high oxygen consumption of body wall tissue and its dependence upon environmental oxygen partial pressure determine the Q_{O_2} of the intact sea urchin; there is thus no need to invoke regulation.

Data concerning the recovery of *S. purpuratus* after periods of oxygen stress and air exposure may also be explained by high body wall respiration. During exposure to air the tube feet, normally extended during submergence, are collapsed. This greatly reduces the transport of oxygen across the tube feet to the water vascular system, and to the internal tissues. This subjects such tissues, which are adapted to low ppO_2, to almost anaerobic conditions. The outer surface of the body wall, while moist, and the inner surface—to the extent it is reached by diffusion of oxygen from the air—have abundant oxygen available during air exposure.

In contrast to total recovery from air exposure after return to air-saturated sea water, recovery of *S. purpuratus* from exposure to low ambient oxygen in sea water (below 80 mm Hg) for more than one or two hours is generally poor. Fewer than 10% of the *S. purpuratus* exposed to periods of oxygen stress remained alive for more than three days following their replacement into aerated aquaria. Periods of oxygen stress initiate the breakdown of the outer body wall in *S. purpuratus*, as evidence by the loss of spines, the lack of normal extension of the tube feet, and the release of echinochrome into the water.

Summary

1. The rate of respiration (Q_{O_2}) of the sea urchin *Strongylocentrotus purpuratus* measured with an oxygen electrode parallels but is somewhat lower than that determined manometrically on the same individuals under the same conditions. The higher values of the Q_{O_2} obtained manometrically are attributable to the higher partial pressure of oxygen (ppO_2) in the fluid of the manometric vessels continuously equilibrated with air as compared to the closed chamber used with the oxygen electrode, in which the ppO_2 is continuously falling.

2. The effects of a number of factors on Q_{O_2} were determined: ppO_2 (including oxygen enrichment), relation between ambient oxygen partial pressure (AO_2), perivisceral oxygen partial pressure ($PvfO_2$) and effect of body size on Q_{O_2}, oxygen consumption of isolated and intact body wall; and the main thrust of this investigation—the change in oxygen consumption during the reproductive cycle.

3. The sea urchin is an oxygen conformer, its oxygen consumption being dependent upon the oxygen partial pressure from above-air saturated partial pressure following enrichment with oxygen down to 10 mm Hg. The oxygen partial pressure of the perivisceral fluid is also dependent upon the ambient oxygen partial pressure. The strict conformity of body wall tissue is the determining factor in the response of the whole body Q_{O_2} to ambient oxygen partial pressure. Internal oxygen partial pressures are the result of low internal oxygen availability after the body wall oxygen demand has been met, and do not determine the whole body Q_{O_2} in *S. purpuratus*.

4. *S. purpuratus* exhibits no systematic change in the Q_{O_2} as the reproductive cycle (as measured by the gonad index) reaches its peak, although the data

are quite variable. Relatively low perivisceral fluid oxygen partial pressures obtain throughout the year, and the gonadal tissue is under a nearly anaerobic condition at all times. The low oxygen availability to the gonadal tissues results in their having little input into the whole body Q_{O_2} of the sea urchin.

5. *S. purpuratus* cannot withstand ambient oxygen partial pressures below the 80 to 100 mm Hg level for more than one or two hours due, apparently, to the sensitivity of the body wall to attenuated ambient oxygen. This is an important factor in restricting this species to habitats near the air saturation level of ppO_2.

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